The implications of territoriality for the social system of the European pine marten *Martes martes* (L., 1758)

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Abstract

The social organisation and the structure of a population of pine martens in the northern part of a low mountain range in northwestern Germany are investigated in a long-term study. Observations by radio-tracking and data from capture-recapture of 12 pine martens (6 females, 6 males) show at least four differences in territory size: the seasonal, the intersexual, that due to the mating system, and that due to genesis.

The territories are held over several years. Males already create summer territories in early spring, before the birth of the offspring and about 5 months before the mating season. They leave these only in late autumn and move into their winter territories. This extensive seasonal territorial behaviour cannot only be explained as mate guarding, but also as offspring guarding by creating a territory-tie. Genetic paternity could be determined by the DNA-fingerprinting method. Parental care of the young by the territorial male was never observed. But males show a distinct guarding behaviour by creating a territorial tie. This social structure is called a male-mother-family.

Introduction

As a number of related Mustelidae species, the pine marten possesses a delayed implantation (Aubert and Canivenc 1986), so that the mating season and the birth of the young lie about 8 months apart. The question is how the male manages to assure his reproductive success in both seasons.

Pine martens are stenotopic silvicolous carnivores, lead a solitary life and occupy intrasexual territories. A male territory can overlap the territory of one or more females (Schröpfer et al. 1989).

In fact, a solitary life seems to be in opposition to a social organisation of both sexes and consequently also to social organisation. Such questions were mainly dealt with in ornithological observations and discussions (Davies 1991). Observations of mammals can hardly be found (Clutton-Brock 1991; Clutton-Brock and Harvey 1978).

For this investigation, it is supposed that the specific territorial behaviour creates an intersexual territory-tie and a specific social organisation that assures the fitness of both sexes.

Material and methods

Study area

The observation area is a forest region, Osnabrücker-Hügelland, lying in the western part of the low mountain range on the southern border of the lowland plain of northwestern Germany. With heights from 85 m to 163 m above sea-level, it belongs to an area of the planar to hilly level. In this region with

a moderate sub-oceanic climate, there is a yearly rainfall of about 800–850 mm; the average humidity is 82% and the fluctuation in yearly temperature is 16.3 °C on average, while the mean temperature in January is 1.0 °C and in July 16.9 °C.

Only a small part of this area is covered by potentially natural vegetation, such as mixed forests of red-beech and oaks (*Fago-Quercetum*), a forest of oaks and birches (*Betula-Quercetum*) or a forest of alders and ashes (*Fraxino-Alnetum*), forming together 16.4%. The proportionately largest area is now formed by spruce forests (*Picea abies*) with 69%, by a cultivated area of larches (*Larix decidua*) 7.5%, by pine forests (*Pinus sylvestris*) 6.6% and by Douglas spruces (*Pseudotsuga menziesii*) 0.5%. According to Palsterkamp Forestry Office records, it can generally be stated that almost 50% of the whole area consists of spruce trees up to forty years of age 45% up to eighty years and 5% over eighty years of age.

The shape of the forest resembles an extended rectangle, from east to west extending about 10 km and from north to south about 2.5 km. In the north, there are some isolated forest islands where pine martens also occur.

Individuals and methods

In this long-term project, pine martens have been caught in live traps (single door boxes constructed in the Dept. of Biology) since the summer of 1987 during operations carried out over several days or weeks.

Constitution, reproductive stage (the size of the praeputial gland field, of the testes and of the nippels) and determination of the age (the weight and the condition of the teeth) were thoroughly tested each time. Each individual was marked with an ID-chip (EuroID, Weilerswist, Germany) for later recognition and for radio-tracking it received a collar-transmitter (motion detector, 150.150 MHz, Karl Wagener-Senderbau, Cologne, Germany) representing about 2% of body weight. The receivers were built in the electronics workshop of the University's Department of Biology/Chemistry. Several 12-channel pocket-receivers with portable antennae (HB 9 CV) and 2 receivers installed on cars were employed. When the animals were in hollows, they could only be tracked from a distance of a few metres. In tree-tops, their most frequent resting places, they could be tracked from a maximal distance of 5 km.

In capture-recapture operations of the 12 animals (6 males, 6 females) some could only be caught once (6 animals) others twice and more often (6 animals; partly up to 11 times). Most pine martens were observed over a few months, or over a few years, and one female almost continually over a 9 year period.

Direct observation of the animals was seldom possible. Therefore, the observational method consisted of two procedures: 1) the animals were located by means of the receiver signal, and their resting place was mapped; or 2) the animals were tracked at certain intervals throughout the night in order to determine their activities and to track the distance they covered. Their day resting sites were mapped noting the tree in which the marten was sleeping. Because of the shape of the forest region, the distance of the located animals was only about 100 m, therefore the tracking location could be noted up to within a few square metres. Tracking and habitat maps were established for each pine marten, which was possible even when it was caught only once. The mapped data and the observational data were recorded and analysed with the McPaal 2.0 programme (Smithsonian Institution, 1988). In addition to the observation points, the forest bounds and other structures of the study area were recorded, when thought to be helpful. By means of the programme, the area sizes (Minimum Convex Polygon MCP) were calculated. It must be stressed that only the locations of day resting sites, and not the locations of tracking observations at night, were included in the calculation of the territory sizes. A track unit was the distance covered by an individual in one night, measured when leaving the resting place in the evening until taking up the same or another resting place the morning thereafter. This method was used in summer as well as in winter. The observation series could cover one to eight nights. The latter was intended to give information about how intensively the martens roam the area in successive activity phases.

Furthermore, pine martens captured by hunters in northwestern Germany were measured for a constitutional analysis. Data were gained from these animals which cannot be obtained from live catches, especially for the determination of age and the reproduction analysis. As the pine martens from the observation area do not differ in size from other individuals of northwestern Germany (t-test = 0.238, df = 86, p = 0.81), the more representative sample was used for the representation of proportions of body sizes.

The determination of paternity was performed with the DNA fingerprinting method. Tissue material used for DNA extraction included bone fragments (WIEGAND et al. 1992) from the feet (metatarsalia)

of the dead animals and blood from the tail vein of the pine martens caught alive. The extracted DNA was quantified fluorimetrically (BONTEMPS et al. 1975). The degree of DNA degradation was investigated using 1.0% agarose gels with subsequent ethidium bromide staining (SAMBROOK et al. 1982). After digestion (restriction enzyme: Hinf I) the DNA was transferred by Southern-blotting onto a nylon membrane (Hybond N, Amersham, UK) according to BRINKMANN et al. (1991). Probe hybridisation was carried out using the radioactive labelled multi locus probe MZ 1.3 (Biotest, Germany). MZ 1.3 was isolated from a human genomic library which had been constructed from DNA partially digested with Sau 3 A. The repeat structure showed a 27 bp repeat unit which was approximately 40 times repeated (SCHACKER et al. 1990).

Autoradiographs of different exposure times were prepared from each blot, because the loading of equimolar DNA concentrations in each lane was not possible, due to varying extraction amounts depending on the tissues used. Two commercially available DNA size standards were used: DNA Analysis Marker (Promega, USA) and Drigest III lambda phage marker (Pharmacia, Germany).

From the autorads only the bands >3 kb were analysed (JEFFREYS et al. 1985). The comparison of band patterns was done manually. A total of 34 different band positions could be determined for all animals by comparing these positions to the band positions of the individual patterns (so-called "present-absent matrix" – KIRBY 1990; GILBERT et al. 1990). All individual DNA patterns in this group were compared in pairs, leading to 45 comparisons for 10 animals. For the calculation of the band sharing rate, the formula $2N/a + b$ was used (N = number of corresponding bands between 2 individuals, a + b = number of bands from individual a + b) (JEFFREYS et al. 1985).

Additionally, a cluster analysis was carried out (UPGMA-method = unweighed pairs between groups; average linkage analysis) using the present-absent matrix of the individual band patterns (GILBERT et al. 1990).

Results

The observations lead to the supposition that the females and the males behave differently in the arrangement of their territories. The two females that could be observed over the longest period, F1 and F6, reduced their territories during these years: at subadult age (approximately in the second summer) the female F1 occupied a territory that was about 8 times as large as that in her fourth and fifth year. She settled in the western part of the territory which she had previously occupied, after having reduced it constantly (y = 545.2 – 96.5x; r = –0.86; p < 0.001; n = 6) (Fig. 1). In this territory of only about 70 ha, the female could be observed during the breeding of 5 litters. The female F6 behaved very similarly:
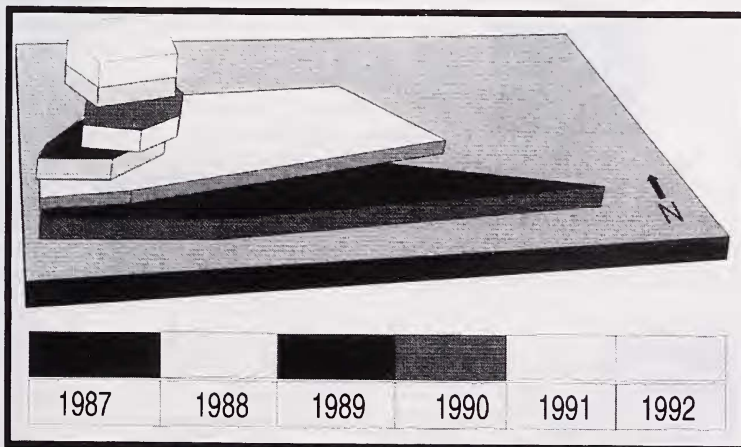

Fig. 1. Changes in size and location of the territories (territory-genesis) of the female F1 over 6 years (Starting at the bottom with the plateau representing the forest area)

she reduced her territory from almost 500 ha to 100 ha from the first winter during the summers until the third winter of observation (y = 638 – 129.7x; r = –0.9; p < 0.001; n = 4). It could be shown that she had her first litter in the second summer. At that time she occupied 250 ha. Before F6 settled in this area, the female F2 had lived there for four years followed by F4 which occupied the area for two years; both had their offspring there. The summer territories had similar sizes of 230 ha and 207 ha, respectively. The female F4 could be observed over two summers and two winters. The two summer territories were of the same size (206 ha and 207 ha, respectively); but she transferred her territory totally to the west in the second summer and had her offspring in the territory left by F2. She reduced her territory each winter: the first time to 153 ha and the second time to 58 ha. However, it must be borne in mind that in the first summer the female was subadult. The long-term observations lead to the conclusion that the females in fact only occupied a territory of a size necessary for themselves and the care of their young.

Up to now, only two of the six males could be observed over a longer period. But in their case it could clearly be seen that their summer territories were much larger than the winter territories (Fig. 2). This does not apply to the females (Mann-Whitney-test: z = –0.05; p = 0.9; n = 16). Although the male R1 lived in a closed forest of which the other male R2 occupied only a small part, the rest being composed of some isolated forest islands, they did not differ in their behaviour. The summer territory of R1 included two female territories, the territory of R2 only one. The location and the expanse of one of R1's summer territories with a size of 1,240 ha led to the supposition that it included 3 female territories, although the presence of a third female could not be proven by trapping. The smaller winter territories of the males were situated either between the female winter territories or enclosed an existent female territory. In an intersexual comparison, the males' summer territories are larger than the females' (Mann-Whitney-test: z = –2.9; p = 0.004; n = 15). The same applies to the year-long territories, if the winter territories are also taken into account (Mann-Whitney-test: z = –3.9; p < 0.001; n = 26).

As the female cares for the young during the summer months and the mating season occurs in midsummer, the sizes of the summer territories are especially of interest in terms of reproduction. A comparison on the basis of sexual dimorphism of body size and
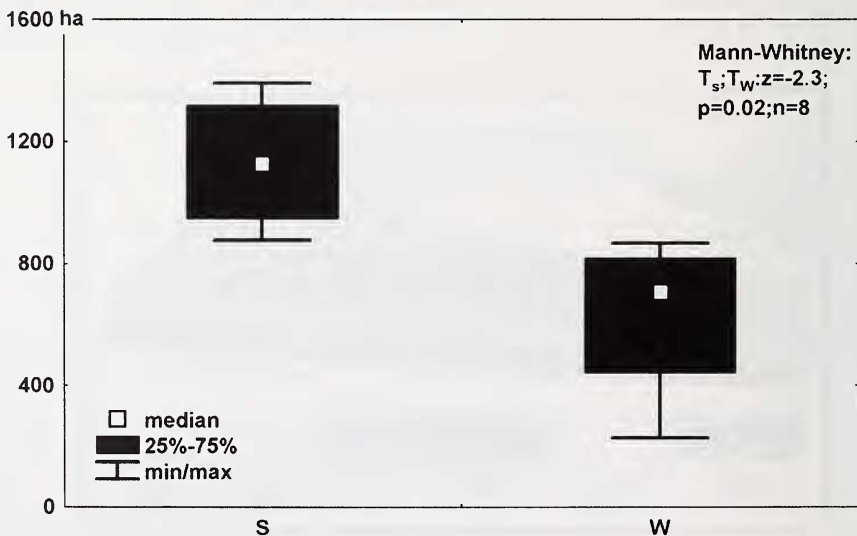

Fig. 2. Size (ha) of the summer and winter territories (T) of the two males R1 and R2 (S: summer, W: winter)
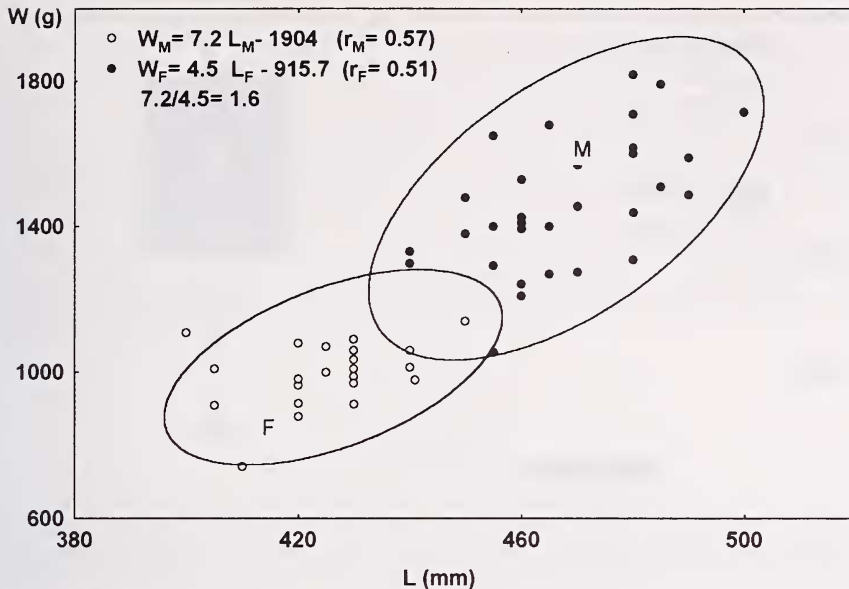
Fig. 3. Size-functions and size-index of the pine marten in northwest Germany
(M: male, F: female, W: weight, L: head-body length, 95%-ellipse)

territory size shows that there is no equal proportion between both: the males are 1.6 times larger than the females, according to a function index calculated on body length and body weight (Fig. 3); whereas the male territories are about 4 times as large as the female territories. Consequently, calculated on the basis of 11 female summer territories, a male summer territory should have a nominal size of 257 ha; but the mean size of 4 male summer territories was actually 1,126 ha. This means that in summer the males occupied a proportionally much larger territory than the females.

It should be noted in this context that the size of the male territory was not just the sum of the enclosed female territories. Female territories did not have common boundaries or were arranged irregularly. The male managed to encompass existing, geographically favourable female territories, the result of which was a polyterritoriality.

This difference in female and male behaviour is confirmed by the tracks observed at night. Their respective locations were gained and analysed independently of the locations of day-resting sites. The distances covered by the male R1 during the summer months were much longer than those of the females F1 and F4 (t-test: $t = -8.06$; df = 54; $p < 0.001$). The intersexual differences in territory sizes correspond to the differences in the distances covered at night, the ratio of which is $1:4.5$ in favour of the male. This also corresponds to the fact that the male R1 covered much greater distances in summer than in winter (Fig. 4). It shows the male's great roaming endurance. On average, he covered a distance of 10,808 m during summer nights; the longest track of the male R1 in one night during a mating season was 18,000 m.

As observations in enclosures suggest that a male "on tour" in summer scent-marks certain points, he probably scent-marks his territory during night activity. The question is whether he manages to keep away rival males from his territory by this extensive marking behaviour. As far as reproduction success is concerned, this could be checked by a paternity determination with DNA-fingerprinting for the male R1 with the offspring of each female F1 and F2. The cluster in the dendrogram (Fig. 5) shows that the territorial male R1 was in fact the only eligible male during the mating season for both female territories.
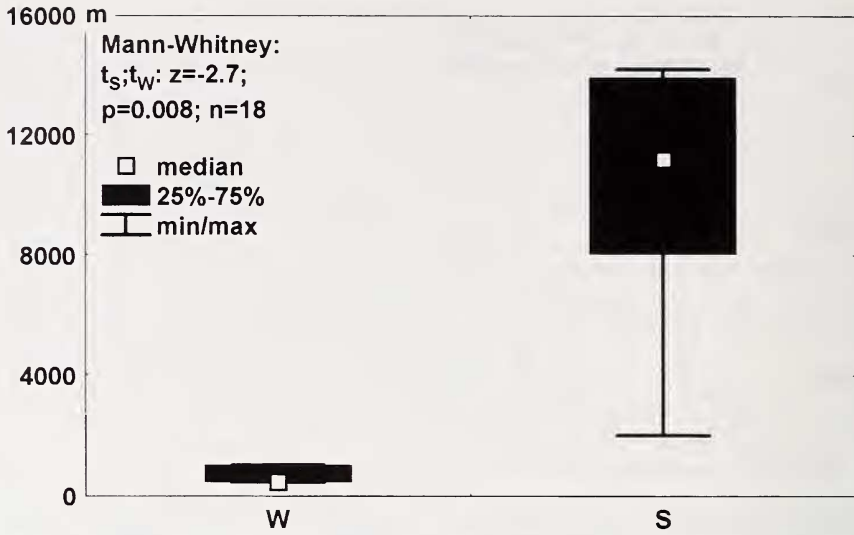
Fig. 4. Length (m) of the winter and summer tracks (t) of the male R1 (S: summer, W: winter)
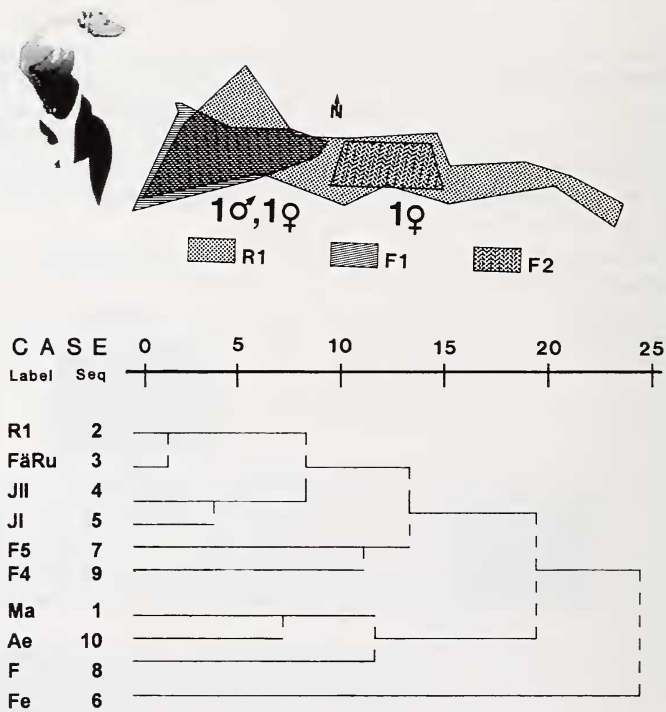

Fig. 5. The paternity of the male R1 with regard to the siblings JI and JII, offspring of the female F1, and the daughter FäRu of the female F2 (MPGMA-method). (Respective territories are illustrated; F4, F5, Ma, Ae, F, Fe: 6 pine martens of other parts of the forest area and of the northwest of Lower Saxony)

This male R1 stayed in the area for 5 years. In the second spring after his disappearance two strong males, about 4 years old, appeared unexpectedly in the area within 2 months (February and March) – R3 (1,745 g) and R4 (1,667 g). R3 could only be observed for 3 days and R4 only for a fortnight. Since that time they have not been trapped again. Instead, a new male R5 (1,517 g), about 3 years old, settled in the western part of the territory previously held by the male R1, where the female F1 lived. A similar occurrence was noted in the territory of R2: after this individual was killed on the road, his territory was taken over by the 3 year-old male R6 (1,637 g).

From the parental analysis and the chronology in which the forest habitat was occupied by the males and the females, it can be deduced that the resident males obviously succeeded in defending their territories intrasexually; but intersexually territories typically overlap for several years.

Discussion

As the study shows, there are at least four differences in territory size: the seasonal, the intersexual, that depending on the mating system and that depending on the genesis.

Thus, the intrasexual territoriality of the pine marten described by SCHRÖPFER et al. (1989) has been confirmed. The territories of adult individuals of the same sex do not overlap, or only partly; and the territories of the males are larger than those of the females.

Direct comparisons of absolute territory sizes given in publications can very rarely be drawn. It is very important to specify the method used for the calculation, as well as the seasons in which the observation was performed. The available data were either collected by means of snow-tracking in winter (PULLIAINEN 1980, 1982, 1984) or by radio-tracking during other seasons (CLEVENGER 1993; KRÜGER 1990; STORCH 1988). Data collected over the entire year are rare (MARCHESI 1989; BALHARRY 1993).

Some relations in territory size correspond approximately to those mentioned here. SCHRÖPFER et al. (1989) found that the ratio of female to male territory is 0.33. In this study the proportion is 0.2. Because in most cases the summer territories also determine the maximum area size within one year (SCHRÖPFER et al. 1989), the literature can be consulted for information concerning the territories occupied throughout the year. MARCHESI (1989) gives details for the Swiss Jura with a ratio of 0.3 (MCP). BALHARRY (1993) reports data from two areas of observation in Scotland, won by tracking. According to the medians, a value of 0.3 and 0.6, respectively, was calculated. According to STORCH (1988) the values are 0.37 and 0.58, comparing winter to summer territories.

The low value of 0.2 for the female territories in the area of northwestern Germany is not the consequence of larger male territories but can be explained by the observation that the female territories were reduced to a minimum size in the third and fourth summer (minimising of territory size).

The intersexual differences in territory size can also be looked at from the point of view of the hypotheses of basis energy (MCNAB 1963). Thereupon, SANDELL (1989) studied numerous solitary carnivore species. According to SANDELL's (1989) calculations the value 2.47 ± 1.06 is in favour of the male territories. The value of 4 found for the observed males lies above the standard division. All this points to the fact that the pine marten male attempts to make its summer territory as large as possible (maximising of territory size). This territory size probably has nothing to do with a higher metabolism, i.e. a greater food availability (see GITTLEMAN and HARVEY 1982). Even in the summer in which the male R1 could monopolise only one female, the male covered about 800 ha, even though the female territory was only 70 ha and was situated on the periphery of the male's terri-

tory. In this case the close proximity of a rival male was probably the reason for the large territory size.

Relatively large male territories, therefore, do not contradict the data concerning the small number of females that were found with the male pine martens. As in the literature (Marchesi 1989; Storch 1988; Balharry 1993), and also in the present study, only 1 or 2 female(s) for each male could be counted. It is probable that this did not seldom lead to a monogamous instead of a polygamous (bigamous) mating system. As monogamy here depends on the accessibility of females, it is a facultative monogamy according to Kleiman's (1977) mating categories. This situation relates to the male; for the female, it is always a monogamous relationship (see Wickler and Seibt 1983).

It is remarkable that in the literature only one female is repeatedly allotted to each male territory in the pine marten, although polygyny is common in the Mustelidae (Moors 1980). The forest habitat with its spatial heterogeneity and free spaces, which makes mate guarding more difficult, may have some influence here. As the determination of paternity shows, the male seems to manage mate guarding in the case of 2 females. This can only be understood by citing the intensive marking behaviour of this marten species as an explanation. The existence of preputial gland fields makes this possible (Stubbe 1969; Monte and Roeder 1990 a). Observations in enclosures have clearly shown that both sexes, but particularly the male, scent-mark intensively as early as spring (Goethe 1964; Monte and Roeder 1990 b, 1993). By means of this territorial marking behaviour of the male, a territorial tie is formed between male, female and offspring.

This assumption is emphasised by the fact that the male already creates the summer territory in early spring, long before the mating season begins (Schröpfer et al. 1989). This period, determined here by tracking, coincides with the increase in testosterone-level in spring, noted by Balharry (1993). That is the reason why the male establishes the summer territory before the birth of its offspring. As our own observations show, the male keeps its summer territory well up to November; only thereafter reducing it. The existence of the summer territory over about 8 months ("pine marten summer") coincides with the very slow development of the young, which are independent only at the beginning of the winter, a characteristic of pine martens and not found in other Mustelidae species (Schmidt 1934, 1943; Heptner and Naumov 1974; own observations).

According to the definition of paternal behaviour, direct care of the offspring is presupposed (i. e. supply with food), but this paternal care cannot be observed in the case of the male pine marten (Schmidt 1943; own observations). Thus, it must be concluded that while the territorial male is the genetic father it is not the parental father, and therefore one cannot speak of a parental family. Nevertheless, the territorial behaviour of the male offers protection for its offspring. Hence, this social system, with reference to Degener's (1918) detailed system of social forms, can be termed a male-mother-family system. This definition appears to deal best with all aspects of care behaviour in this solitary marten species.

Acknowledgements

Zusammenfassung

Die Bedeutung der Territorialität für das Sozialsystem des Europäischen Baummarders Martes martes
(L., 1758)

In einer Langzeitstudie werden die soziale Organisation und die Struktur der Population von Baummardern in der nördlichen Mittelgebirgsstufe Nordwestdeutschlands untersucht. Die telemetrischen Beobachtungen und die Fang-Wiederfangdaten von 12 Baummardern (6 Fähen, 6 Rüden) lassen in der Territoriumsgröße einen saisonalen, einen intersexuellen, einen vom Paarungssystem und einen von der Territoriumsgenese abhängigen Flächenunterschied erkennen. Einem Körpergrößen-Unterschied von 1,6 von Fähe und Rüde steht ein Vierfaches der Territoriumsgröße des Rüden gegenüber.

Die Territorien werden über mehrere Jahre besetzt gehalten. Da die Rüden schon im zeitigen Frühjahr vor der Geburt der Jungtiere und ca. 5 Monate vor der Ranzzeit die Territorien einrichten, und diese erst im Spätherbst aufgeben (Baummarder-Sommer), um die Winterterritorien zu beziehen, wird dieses jahreszeitlich ausgedehnte territoriale Verhalten nicht nur als ein Partner-Hüten sondern auch als ein Jungtier-Hüten durch Territorien-Bindung erklärt. Mit DNA-fingerprinting konnte zwar genetisch die Vaterschaft nachgewiesen, eine elterliche Wurfpflege des territorialen Rüden aber niemals beobachtet werden. Da er jedoch das ausgeprägte Hüteverhalten durch territoriale Bindung zeigt, wird diese Sozialstruktur als eine Mann-Mutter-Familie bezeichnet.

References

Aubert, I.; Canivenc, P. (1986): Nidation différée chez les mustélides: Étude ultrastructurale utéro-blastocytaire chez le blaireau européen, la matre et la fouine. Arch. Biol. (Bruxelles) **97**, 157–186.

Balharry, D. (1993): Social organization in martens: an inflexible system? Symp. Zool. Soc. Lond. **65**, 321–345.

Bontemps, J.; Houssier, C.; Fredicy, E. (1975): Physico-chemical study of the complexes of '33 258 Hoechst' with DNA and nucleohistone. Nucleic Acids Res. **2**, 971–985.

Brinkmann, B.; Rand, S.; Wiegand, P. (1991): Population and family data of RFLP's using selected single- and multi-locus systems. Int. J. Legal Med. **104**, 81–86.

Clevenger, A. P. (1993): Pine marten (*Martes martes* L.) home ranges and activity patterns on the island of Minorca, Spain. Z. Säugetierkunde **58**, 137–143.

Clutton-Brock, T. H. (1991): The Evolution of Parental Care. Princeton: Princeton Univ. Press.

–; Harvey, P. H. (1978): Mammals, resources and reproductive strategies. Nature **273**, 191–195.

Davies, N. B. (1991): Mating systems. In: Behavioural Ecology. Ed. by J. R. Krebs and N. B. Davies. London: Blackwell SP. Pp. 263–294.

Degener, P. (1918): Die Formen der Vergesellschaftung im Tierreich. Leipzig: Veit und Camp.

Gilbert, D. A.; Lehman, N.; O'Brien, S. J.; Wayne, R. K. (1990): Genetic fingerprinting refects population differentiation in the California Channel Island fox. Nature **344**, 764–767.

Gittleman, J. L.; Harvey, P. H. (1982): Carnivore home-range size, metabolic needs and ecology. Behav. Ecol. Sociobiol. **10**, 57–63.

Goethe, F. (1964): Das Verhalten der Musteliden. Hdb. Zool. VIII, 10. Teil, 1–80.

Heptner, V. G.; Naumov, N. P. (1974): Die Säugetiere der Sowjetunion. Bd II. Jena: G. Fischer. Pp. 538–571.

Jeffreys, A. J.; Wilson, V.; Thein, S. L. (1985): Hypervariable "minisatellite" regions in human DNA. Nature **314**, 67–73.

Kirby, L. T. (1990): DNA Fingerprinting – an introduction. New York: Stockton Press.

Kleiman, D. G. (1977): Monogamy in mammals. Quart. Rev. Biol. **52**, 39–69.

Krüger, H.-H. (1990): Home ranges and patterns of distribution of stone and pine martens. Trans. Inst. Union of Game Biol., Congr. **19**, 348–349.

Marchesi, P. (1989): Écologie et comportement de la martre (*Martes martes* L.) dans le Jura Suisse. Thèse doct. Université de Neuchatel.

McNab, B. K. (1953): Bioenergetics and the determination of home range size. Am. Nat. **97**, 133–140.

Monte, M. de; Roeder, J.-J. (1990 a): Histological structure of the abdominal gland and other body regions involved in olfactory communication in pine martens (*Martes martes*). Z. Säugetierkunde **55**, 425–427.

– (1990 b): Les modalités de communication chez la martre (*Martes martes*). Mammalia **54**, 13–24.

– (1993): Scent marking and social relationships in pine martens (*Martes martes*). Zoo Biol. **12**, 513–523.

Moors, P. J. (1980): Sexual dimorphism in the body size of mustelids (Mammalia: Carnivora): The role of food habits and breeding systems. Oikos **34**, 147–158.

Pulliainen, E. (1980): Winter habitat selection, home range and movements of the pine marten (*Martes martes*) in a Finnish Lapland forest. In: Worldwide Furebearer Conf. Proc. Ed. by J. A. Chapman and D. Pursley. Pp. 1068–1087.

– (1982): Scent-marking in the pine marten (*Martes martes*) in Finnish Forest Lapland in winter. Z. Säugetierkunde **47**, 91–99.

– (1984): Use of the home range by pine martens (*Martes martes* L.). Acta Zool. Fennica **171**, 271–274.

Sambrook, J.; Maniatis, T.; Fritsch, E. F. (1982): Molecular cloning. A new laboratory manual. Cold Spring Harbour, New York: CSH Laboratory Press.

Sandell, M. (1989): The mating tactics and sparing patterns of solitary carnivores. In: Carnivore Behavior, Ecology, and Evolution. Ed. by J. L. Gittelman. London: Chapman and Hall. Pp. 164–182.

Schacker, U.; Schneider, P. M.; Holtkamp, B.; Bohnke, E.; Fimmers, R.; Sonnneborn, H. H.; Rittner, C. (1990): Isolation of the DNA minisatellite probe MZ 1.3 and its application to DNA 'Fingerprinting' analysis. Forensic. Sci. Int. **44**, 209–224.

Schmidt, F. (1934): Über die Fortpflanzungsbiologie vom sibirischen Zobel (*Martes zibellina* L.) und europäischen Baummarder (*Martes martes* L.). Z. Säugetierkunde **9**, 392–403.

– (1943): Naturgeschichte des Baum- und des Steinmarders. In: Monographien der Wildsäugetiere. Ed. by D. Müller-Using. Leipzig: Schöps.

Schröpfer, R.; Biedermann, W.; Szczesniak, H. (1989): Saisonale Aktionsraumveränderungen beim Baummarder *Martes martes* L. 1758. In: Populationsökologie marderartiger Säugetiere. Wiss. Beitr. Univ. Halle **37**, 433–442.

Storch, I. (1988): Home range utilization by pine martens. Z. Jagdwiss. **34**, 115–119.

Stubbe, M. (1969): Die analen Markierungsorgane der *Martes*-Arten. Acta Theriol. **22**, 303–312.

Wickler, W.; Seibt, U. (1983): Monogamy: an ambigous concept. In: Mate choice. Ed. by P. Bateson. Cambridge: Cambridge Univ. Press.

Wiegand, P.; Rand, S.; Bajanowski, T. (1992): Möglichkeiten der DNA-Typisierung an exhumierten Leichengeweben. Rechtsmedizin **3**, 13–15.

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